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Unveiling the geographic distribution of *Boana pugnax* (Schmidt, 1857) (Anura, Hylidae) in Venezuela: new state records, range extension, and potential distribution

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Abstract

Boana pugnax is a treefrog inhabiting open lowlands from southern Central America and northwestern South America. Its geographic distribution in Venezuela is poorly understood due, in part, its morphological similarity with *B. xerophylla* (with which is frequently confused) and the few localities documented. In order to increase the knowledge of the distribution of *B. pugnax* in the country, we examined the specimens of *B. pugnax* and *B. xerophylla* deposited in 4 Venezuelan museums, compiled the locality records of *B. pugnax*, and generated a model of potential distribution for species. We report 46 new localities for the species in Venezuela, including 8 new state records, which increases considerably its range extension.

Key words

Rana platanera; Chiriqui-flusse treefrog; *Boana faber* species group; Neotropics; species distribution modeling.

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Introduction

Boana pugnax (Schmidt, 1857) is a nocturnal, medium-sized treefrog, inhabiting in open lowlands of southern Central America and northern South America (Frost 2017). Its type locality is "along the Chiriquí rivers not far from Bocas del Toro" (Panama) according Kluge (1979). This species has a discontinuous pattern of geographic distribution, ranging from central Panama, with a hiatus in eastern Panama and western Colombia, and continuing through northwestern Colombia to northwestern Venezuela (Kluge 1979, La Marca 1996, Mijares-Urrutia and Arends 1999, Duellman 2001, Lynch and Suárez-Mayorga 2001, La Marca et al. 2010), between 5 and 540 m above sea level (a.s.l.) (Lynch and Suárez-Mayorga 2001).

Boana pugnax was resurrected from the synonymy of *B. crepitans* (Wied-Neuwied, 1824) by Kluge (1979), and both species were proposed as members of *B. faber* group (Faivovich et al. 2005). Recently, Orrico et al. (2017)

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resurrected *B. xerophylla* (Duméril & Bibron, 1841) from the synonymy with *B. crepitans*. They defined as *Boana xerophylla* all the populations previously referred as *B. crepitans* from eastern Panama, Colombia, Venezuela, the Guianas, and northwestern Brazil. *Boana pugnax* and *B. xerophylla* are found in sympatry in some localities in Central America and northern South America (Kluge 1979, Lynch and Suárez-Mayorga 2001), and they are frequently confused due its morphological similarities (La Marca 1996), particularly when are preserved. Consequently, numerous specimens of *B. pugnax* deposited in Venezuelan museums have been previously misidentified, and the current knowledge about its geographic distribution is limited.

In Venezuela, *B. pugnax* was recorded for first time by La Marca (1996), based on a single specimen (ULABG 3292) from south of Maracaibo Lake Basin (Mérida state). Subsequently, Mijares-Urrutia and Arends (1999) documented a new locality for this species in Falcón state, northern Venezuela, and Chacón-Ortiz et al. (2004) referred it from Táchira state in the eastern piedmont of the Andes (Orinoco basin). The species also was referred by Barrio-Amorós (2004) for the Venezuelan Llanos, but neither precise locality nor voucher specimens were mentioned. Tárano (2010) described the vocalizations of *B. pugnax* from Guárico state in the Central Llanos from Venezuela, and recently Infante-Rivero and Velozo (2015) recorded this species for the Zulia state, at west Lake Maracaibo. Here we aimed to increase the knowledge about the geographic distribution of *B. pugnax* in Venezuela. After a review of 4 Venezuelan museums, we report new state records and distribution extensions for *B. pugnax* in the country. Additionally, we developed a species distribution model, in order to increase the knowledge of the distribution of this species, as well as identify gaps in the potential distribution.

Methods

Venezuelan records of *B. pugnax* were obtained from the following Venezuelan museums: Colección de Anfibios del Laboratorio de Biogeografía de la Universidad de Los Andes (ULABG), Mérida; Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Ciencias Naturales de Guanare (MCNG), Guanare; and Museo de Historia Natural La Salle (MHNLS), Caracas. We verified the identity of all specimens of MHNLS identified as *B. pugnax*, *B. xerophylla* (previously *B. crepitans,*) and *Boana* sp., and all specimens identified as *B. xerophylla* and *B. pugnax* in the other 3 collections, in order to detect specimens of *B. pugnax* yet unidentified or misidentified, and to recover as many records as possible.

We followed the morphological definition and diagnosis established by Kluge (1979), and Duellman (2001) to identify the specimens as *B. pugnax*. According these authors and Orrico et al. (2017), adult males of *B. pugnax* are larger than *B. xerophylla* [68.9–77.9 mm vs 42.9–63.8 mm of snout-to-vent length (SVL), respectively]. Further, the former species has less pigmentation in the anterior half of palpebral membrane, has darker and thicker bars on the pleural region, and dark bars on the anteroventral surface of thighs (Fig. 2). We also considered the differences in throat pigmentation noted by La Marca (1996) between *B. xerophylla* and *B. pugnax* from western Venezuela: unpigmented in *B. xerophylla* and blackish-brown colored in *B. pugnax* (Fig. 2). These morphological definitions are congruent with molecular (DNA sequences) and acoustic (advertisement calls) evidences obtained previously with specimens from western Venezuela (M. Escalona et al., unpublished data).

We generated the species distribution model (SDM) for *B. pugnax* based on all the locality records from Venezuela obtained from the museums listed above and from literature (La Marca 1996, Mijares-Urrutia and Arends 1999, Chacón-Ortiz et al. 2004, Tárano 2010), whereas those from Panama and Colombia were compiled from the Círculo Herpetológico de Panama's webpage (Círculo Herpetológico de Panamá 2017), Batrachia online database (Acosta-Galvis 2017), and literature (Kluge 1979, Lynch and Suárez-Mayorga 2001, Armesto et al. 2009, Mendez-Narvaez et al. 2014, Guarnizo et al. 2015). We did not include the records of GBIF due to difficulty of verifying the identity of specimens on which those records are based and we presumed the occurrence of an important number of misidentifications (see below). Each locality was verified and georeferenced (when necessary) using Google Earth®. All geographic coordinates were transformed in decimal degrees, based on the WGS 84 datum.

We performed the SDM under the Maximum Entropy algorithm in MaxEnt version 3.3.3k (Phillips et al. 2006) due to its better proved performance, including a lower commission error (i.e., overestimating) in the models (e.g., Elith et al. 2006, 2011, Peterson et al. 2007). We used interpolated climate data from WorldClim project (Hijmans et al. 2005) and the terrestrial ecoregions (Olson et al. 2001), both at 30″ resolution (~1 km^2 cell size), as input variables in order to characterize the ecological niche and potential distribution of the focal species. Bioclimatic layers were cropped to include latitudes 01.1947° N to 12.4193° N and longitudes 089.8861° W to 059.9454° W. Despite the fact that categorical variables, such as ecoregions or ecosystems are not commonly used in SDM studies, we decided to include it because this predictor may be considered as variable related directly with the ecology of the focal species (Pearson and Dawson 2003, Austin 2007, Rödder et al. 2009, Jiménez-Valverde et al. 2011). Thus, the obtained models provide a first approximation indicating the better hypotheses for the potential distribution of *B. pugnax* at the current time.

We used a geographical clip (Fig. 1) based on the intersection of Terrestrial Ecoregions (Olson et al. 2001) and the Biogeographical Provinces of the Neotropic (Morrone 2014) in order to create an area for model calibration (or M sensu BAM diagram; see Soberón and Peterson 2005, Barve et al. 2011). In addition, for a first

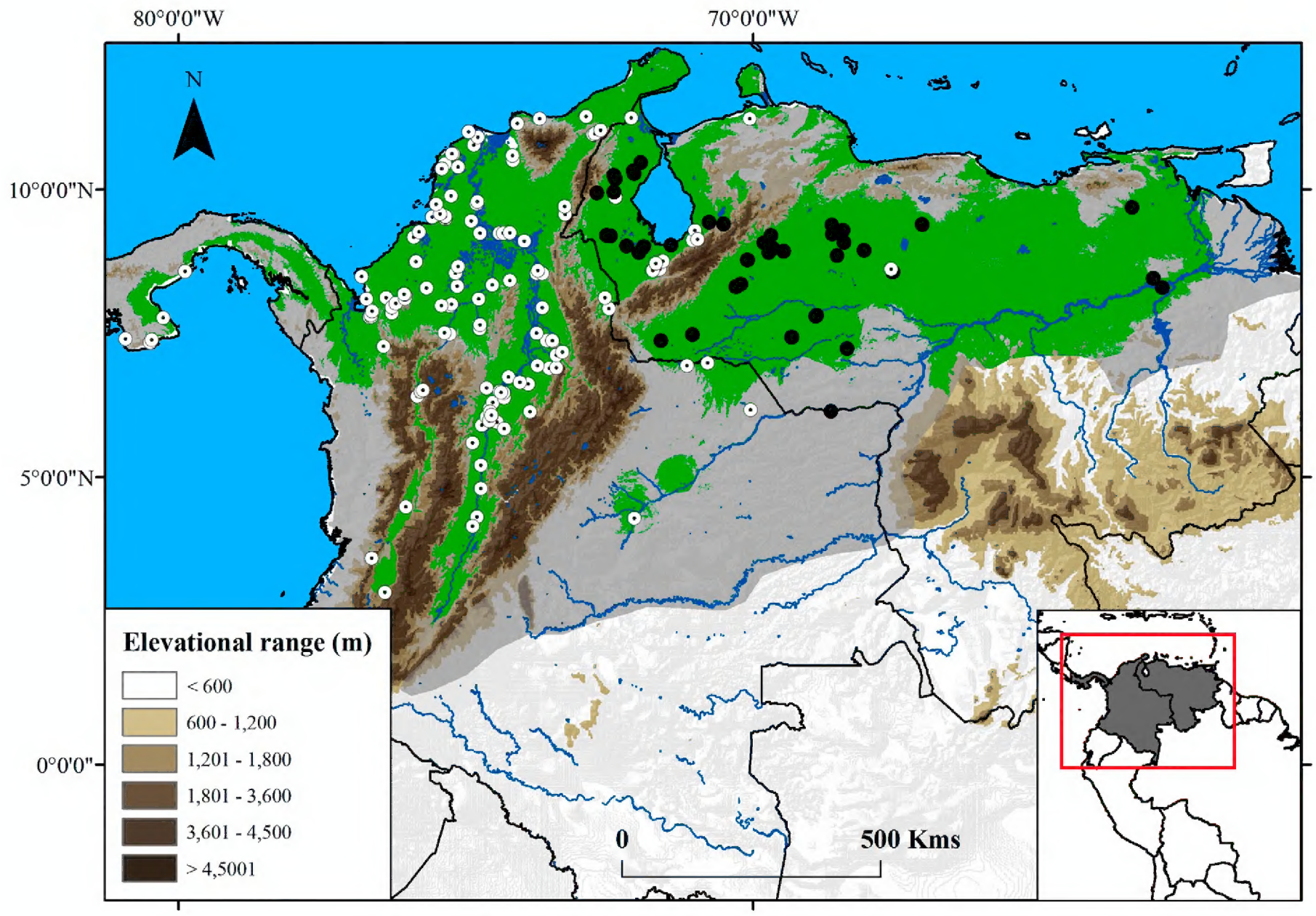

Figure 1. Species distribution model (SDM) and locality records of *Boana pugnax*. White-with-black-dot circles: literature records from Kluge (1979), La Marca (1996), Lynch and Suárez-Mayorga (2001), Armesto et al. (2009), Tárano (2010), and Guarnizo et al. (2015). Black circles: new records based on museum data. Gray area: calibration area (see Soberón and Peterson 2005, Barve et al. 2011) used in the SDM reconstruction. Green area: Potential SDM with the threshold value of Fixed Omission Value 5 (FOV5).

explorative analysis, we used the 20 bioclimate layers and assessed which variables were the most important for the model, according to the Jackknife test calculated in MaxEnt (Berger 2007, Elith et al. 2011). In a second modelling exercise, we generated the species distribution using non-correlated environmental variables ($r < 0.8$) in combination with the most relevant environmental variables identified in the first approach (e.g., Ortega-Andrade et al. 2015). These additional steps allowed us to reduce the collinearity of variables and over-fitting of the generated distribution models (see Peterson et al. 2011).

The SDM was generated with 80% of the locality records (training data) while the other 20% was used for model evaluation (testing data). We ran 1,000 iterations, with no extrapolation in order to avoid artificial projections of the extreme values of the ecological variables (Elith et al. 2011, Stohlgren et al. 2011). All other parameters in MaxEnt were maintained as default settings. We ran 10 cross-validate replicates to calculate confidence intervals in order to select the best model based on the performance of area under the curve or "AUC" (Elith et al. 2006, 2011).

Then, we used the logistic response to obtain the values for habitat suitability (continuous probability from 0 to 1; Phillips et al. 2006), which were subsequently converted to binary presence-absence values on the basis of the established threshold value, defined herein as the "Fixed Omission Value 5" or FOV5 (Liu et al. 2013). This threshold allowed us to evaluate the species' distribution by minimizing commission errors (i.e., over-predictions) in our final binary maps. Finally, the performance of the selected model was assessed based the commission and omission errors (Anderson et al. 2003) and by applying the Partial-ROC (Receiver Operating Characteristic) curves test (Lobo et al. 2008, Peterson et al. 2008). This criterion was used to solve problems associated with an inappropriate weighting of the omission and commission errors during the AUC analysis (see Lobo et al. 2008, Peterson et al. 2008).

Results

Our study includes new information about the *B. pugnax*'s distribution, with 179 unique occurrences recorded (57 points from Venezuela, 117 from Colombia, and 5 from Panama), including localities quite outside from the recognized geographic distribution range (Fig. 1, Table 1, Table A1). Surprisingly, we found an important number of misidentifications in the Venezuelan museums reviewed (ca 79%). A total of 46 new localities were recorded for first time for Venezuela, extending the geographic distribution of *B. pugnax* ca 852 km east of the closest know locality in the country (Fig. 1, Table 1).

Figure 2. *Boana pugnax* adult male in life (ULABG 7739) from Caño San Mateo (South of Maracaibo Lake Basin, Mérida state, Venezuela). **A.** Dorsolateral view. **B.** Ventral view showing the blackish coloration at throat level. **C.** Color pattern of the flank of body. **D.** Ventral view at thigh, showing its color pattern in preservative. Photos: Ivan Mendoza (A–C) and Moisés Escalona (D).

Discussion

The new occurrences, based on confirmed identification of specimens, include new state records for Apure, Anzoátegui, Barinas, Cojedes, Guárico, Monagas, Portuguesa, and Trujillo. Thus, our new records change considerably the previous statement of *B. pugnax* as restricted to western Venezuela (Duellman 2001, Lynch and Suárez-Mayorga 2001, Chacón-Ortiz et al. 2004, La Marca et al. 2010), and exceed the prediction formulated by La Marca et al. (2010), who suggested that this species was expected to be in Apure, Barinas, and Zulia state.

All the 116 specimens recorded (representing 57 unique localities) for *B. pugnax* in Venezuela are between 0–605 m a.s.l. (Table 1, Appendix Table A1). These records reduce scarcely the elevational range reported previously for Venezuela (0–700 m a.s.l.) by Barrio-Amorós (2004). Other localities documented in Panama are below 100 m a.s.l. (Duellman 2001), while in Colombia are mainly below 500 m a.s.l. (Lynch and Suárez-Mayorga 2001). Thus, this species seems be predominantly from lowlands as suggested Kluge (1979) and Lynch and Suárez-Mayorga (2001). In this sense, it is important to note that our model did not predict 4 localities reported with higher elevation in Colombia (see Table A1): Bitaco, Valle del Cauca, at 1426 m a.s.l. (voucher USNM 151982 [USNM database]); Minca, Magdalena, at 1530 m a.s.l. (Lynch and Suárez-Mayorga 2001); one locality from the Valle del Cuaca, at 940 m a.s.l. and another locality from the Cauca, at 1200 m a.s.l. (Mendez-Narvaez et al. 2014). Despite that we argue the need of validation at field for model in these areas, an alternative explanation for these results may involve the misidentifications for the specimens as we found in the Venezuelan museums (see above).

The predictive potential SDM of *B. pugnax* had a high success-rate for the AUC-test (0.889) and ROC-Partial (1.24 ± 0.22) values, as well as low omission error (17.64%; $N = 7$) for the threshold values (0.103). Thus, the SDM was considered to be statistically significant (Peterson et al. 2008, Elith et al. 2011). The variables that contributed most to the model were mean temperature of coldest quarter (28.7%), mean temperature of wettest quarter (17.7%), temperature seasonality (15.0%), precipitation of wettest quarter (14.2.1%), and isothermality (8.7%); which comprised 84.3% of the contribution for the estimation model (Table 2).

Interestingly, the most important variable found here (i.e. mean temperature of coldest quarter) support the Lynch and Suárez-Mayorga (2001) affirmation that *B. pugnax* may be "... unable to breed in cooler environments...". The *B. pugnax* distribution range (according the FOV5) totalled ~658,400 km^2 along the region from Venezuela to Panama, with ~394,300 km^2 (59.9%) estimated for Venezuela, ~245,400 km^2 (37.3%) for Colombia, and only ~18,700 km^2 (2.8%) for Panama (Fig. 1). These values were greater than previously thought (La Marca et al. 2010). Lynch and Suárez-Mayorga (2001)

Table 1. New state locality records of *Boana pugnax* in Venezuela. Geographic coordinates are provided based on the WGS 84 datum. Source: Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Ciencias Naturales de Guanare at Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora (MCNG), Guanare; Museo de Historia Natural La Salle (MHNLS), Caracas; and the Colección de Anfibios y Reptiles del Laboratorio de Biogeografía de la Universidad de Los Andes (ULABG), Mérida. Abbreviation: a.s.l. = above sea level.

No.	State: locality	Latitude, longitude	Elevation a.s.l. (m)	Source (voucher)
1	Anzoátegui: Mamo	08.4608, –063.0350	75	MHNLS (8701–8707, 8820)
2	Anzoátegui: Sector Punta Cuchillo, around Caimán lagoon, NE Orinoquia bridge, north edge of río Orinoco	08.2933, –062.8824	2	MNHLS (20267)
3	Apure: Modulo Fernando Corrales	07.2333, –068.3666	59	CVULA (3416, 3417); MCNG (168, 169, 647, 651)
4	Apure: Hato El Frío	07.8166, –068.8958	54	MHNLS (7466, 8619–8624, 16315); ULABG (5446)
5	Apure: Paso El Burro	07.3749, –071.6048	199	CVULA (7078)
6	Apure: Hato El Cedral, field near Matiyure camp	07.4298, –069.3250	83	ULABG (7781–7783, 7790–7792)
7	Apure: Caño Negro, 6 km SW Buena Vista	06.1416, –068.6433	59	MHLS (8979–8981)
8	Apure: La Ramera road, Las Ventanas, Hato El Frío	07.8011, –068.9141	54	MHNLS (12112)
9	Apure: Hato El Cedral	07.4350, –069.3261	83	MHNLS (14283, 14792)
10	Apure: Laguna de Derbio, near Hato El Frío's biological station	07.8166, –068.8958	54	MHNLS (16269–16272)
11	Barinas: 40 km S Barinas	08.3567, –070.2095	133	CVULA (502)
12	Barinas: El Irel, Barrancas	08.7715, –070.0976	237	CVULA (2541, 2544, 2551, 2553, 6919); ULABG (5594, 5666, 5668, 6970)
13	Barinas: Reserva Forestal Caparo, experimental station	07.4715, –071.0548	139	ULABG (5594)
14	Barinas: Sector El Moraleño	08.3047, –070.2939	141	MHNLS (21245, 21246)
15	Cojedes: Río Portuguesa, 15 km El Baúl	08.8522, –068.5416	47	MHNLS (1942, 1943, 1945–1947)
16	Cojedes: Hato El Tirado	09.0800, –068.4133	74	MHNLS (6312, 6313, 6323–6325)
17	Cojedes: El Veladero, 100 m SE Las Vegas	09.3833, –068.6333	85	MHNLS (6423–6426)
18	Cojedes: Hato Itabana, 38 km SW Las Vegas	09.2333, –068.4666	77	MHNLS (6462)
19	Cojedes: Hato Los Caballos, 38 km S Tinaco	09.2933, –068.4305	89	MHNLS (6991–6994)
20	Cojedes: Hato Piñero	08.9380, –068.0669	112	MHNLS (12365)
21	Cojedes: Campus Fundación La Salle (FLASA), San Carlos	09.2205, –068.6238	77	MHNLS (13830)
22	Guárico: El Sombrero	09.3872, –067.0533	147	MHNLS (2896)
23	Guárico: Fundo Pecuario Masaguaral	08.5666, –067.5833	72	Tárano 2010
24	Guárico: Hato Masaguaral	08.5644, –067.5644	72	MHNLS (14102)
25	Monagas: Hato La Candelaria, 30 km Maturín	09.6888, –063.4083	82	MHNLS (2945, 2946)
26	Portuguesa: Fundaguanare, Guanare	09.0537, –069.7324	148	MCNG (627)
27	Portuguesa: Mesa de Cavaca	09.0762, –069.8150	285	MCNG (638)
28	Portuguesa: Fundo El Drago	08.9281, –069.4710	98	MCNG (801–803)
29	Portuguesa: Río Tucupido	08.9076, –069.7283	122	MCNG (809)
30	Portuguesa: El Potrero, way to Suruguapo, aprox. 12 km old road Guanare-Acarigua	09.1981, –069.6865	202	ULABG (5367)
31	Portuguesa: Road Guanare-Guanarito, 8 km intersection road Guanare-Barquisimeto	08.9769, –069.6562	128	ULABG (7749, 7750)
32	Trujillo: Sabana de Mendoza	09.4369, –070.7663	166	MHNLS (2955)
33	Trujillo: Between Valera and Trujillo, near fuel station	09.3977, –070.5171	396	ULABG (5704, 5705)
34	Zulia: Santa Bárbara del Zulia	09.0024, –071.8891	9	CVULA (968, 969, 971, 972, 974, 3745, 4531, 4552, 4824)
35	Zulia: Santa Bárbara del Zulia, Malariología's house	09.0083, –071.9050	7	MHNLS (14710)
36	Zulia: Santa Cruz del Zulia	08.9070, –071.9854	10	CVULA (969, 970)
37	Zulia: El Pino	09.0347, –071.4304	21	ULABG (2530, 2531, 2989, 2991)
38	Zulia: Hacienda La Esperanza (La Universidad del Zulia), km 107 road Maracaibo-Machiques	10.1863, –072.3983	108	CVULA (3665)
39	Zulia: Río Yasa	09.9430, –072.7230	156	MHNLS (1580, 2966)
40	Zulia: Hato Los Mangos, Machiques	10.2500, –072.4175	123	MHNLS (9622)
41	Zulia: Caño Caimán, 7 km N Encontrados	09.0200, –072.1939	19	MHNLS (15744–15747)
42	Zulia: Hacienda Grano de Oro, remanent forest, Campo Boscán	10.2711, –072.0683	2	MHNLS (16866, 16870–16873)
43	Zulia: Hacienda Grano de Oro, Campo Boscán	10.4649, –071.9541	96	MHNLS (18602)
44	Zulia: Hacienda Cincelejo, Campo Boscán	10.3230, –072.0891	9	MHNLS (16889, 16890, 16902)
45	Zulia: Hacienda San Martín, Sector Aguas Negras (ancient Juan Manuel's house)	09.1872, –072.4783	31	MHNLS (17946, 17947, 17989, 17990)
46	Zulia: Hacienda Monterrey, Sector Calle Larga	09.9560, –072.4192	104	MHNLS (20330–20333)

Table 2. Summary of the selected, not-correlated, environmental variables with relative contributions (%) to the potential distribution model of *Boana pugnax* using MaxEnt 3.3.3k.

Abbreviation	Environmental variable	Percentage of contribution
Bio 11	Mean temperature of coldest quarter	28.7
Bio 08	Mean temperature of wettest quarter	17.7
Bio 04	Temperature seasonality (standard deviation *100)	15.0
Bio 16	Precipitation of wettest quarter	14.2
Bio 03	Isothermality (bio2/bio7) (* 100)	8.7
Biome	Terrestrial ecoregions	4.7
Bio 19	Precipitation of coldest quarter	3.4
Bio 17	Precipitation of driest quarter	3.0
Bio 07	Temperature annual range (BIO5–BIO6)	2.4
Bio 09	Mean temperature of driest quarter	2.2

mentioned that *B. pugnax* was a near-Colombian endemic species; however, our results suggest that this taxon is more extensively distributed in Venezuela.

Our SDM predicts the presence of *B. pugnax* in 14 ecosystems (Olson et al. 2001) for Venezuela; 4 of them encompass ~90% of its total area estimated in the country. The most extensive ecosystems were the savannah (~190,250 km^2; 48.25% of the extent areas), the dry forests (~84,500 km^2; 21.44%), the xeric shrublands forests (~63,000 km^2; 15.99%), and the Catatumbo moist forests (15,600 km^2; 3.96%). It is important to note that our SDM suggests the presence of *B. pugnax* in additional ecosystems (including moist forests, montane forests, mangroves, wetlands, and swamp) throughout Venezuelan states: Lara, Carabobo, Miranda, Sucre, and Bolívar. All these predictions will need a validation at field. However, the presence in these regions is expected on the base of habitat type and continuity reported in the areas, which is congruent with the species' biology (La Marca et al. 2010).

Additionally, the SDM suggest lowest suitability values throughout the Cordillera de Mérida, the Cordillera Oriental (Eastern Andes in Colombia), and the Sierra de Perijá (northern border between Venezuela and Colombia), which could be interpreted as potential geographic and ecological barriers for the dispersion of *B. pugnax* (Fig. 1). Hence, the change of physical variables along the elevational gradient in these mountains could constrain the spread of individuals through them (Janzen 1967). This is congruent with the allozymatic differences found between populations from northwest and southeast of Cordillera de Mérida (Nava 2005). However, the current evidence let us to treat all populations of *B. pugnax* as a single species. Nevertheless, these disjunct populations could merit the recognition as Evolutionarily Significant Units (ESUs) in the future, which will be important in a biology conservation context (Moritz 1994).

Finally, our results encourage the need to continue studying the biology of *Boana pugnax*, providing an ecological framework of where to focus the future survey efforts in Venezuela, as well as in Colombia and Panama. Modeled distributions have the advantage of filling gaps that point-based distributions present as a result of the necessarily incomplete sampling (Peterson 2001, Mota-Vargas and Rojas-Soto 2012), but at same time identify the most important variables for the species persistence (Soberón and Peterson 2005, Elith et al. 2011). Furthermore, this technique provides better results in terms of spatial and numerical sensitivity as well as lower values of omission and a moderate extent of predicted areas; therefore, are widely used in ecology, evolution, conservation, and management (e.g., Soberón and Peterson 2005, Mota-Vargas and Rojas-Soto 2012, Ortega-Andrade et al. 2015). Additionally, this study illustrates the importance of the museums specimens as a source of data (see Rocha et al. 2014) to increase the knowledge about species' geographic distribution.

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Authors' Contributions

ME and FRR identified the specimens and compiled the database of records; DPT performed the species distribution model; and ME, DPT, and FRR wrote the manuscript.

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Appendix

Table A1. Records of *Boana pugnax* previously reported for Colombia (CO) and Panama (PA), and additional records for Venezuela (VE) analyzed for this study. Acronyms correspond to AMNH: American Museum of Natural History; ANDES-A: Museo de Historia Natural de la Universidad de Los Andes; ANSP: Academy of Natural Sciences; a.s.l.: above sea level; BATRACHIA: Checklist of Colombian Amphibians' webpage; Colombia; CAS: Museum of California Academy of Science; CHPW: Círculo Herpetológico de Panama's webpage; Philadelphia; CO: Colombia; FMNH: Field Museum of Natural History; UMMZ: University of Michigan Museum of Zoology; IAvH: Instituto Alexander von Humboldt; ICN: Instituto de Ciencias Naturales, Colombia; ICNMH: Museo de Historia Natural del Instituto de Ciencias Naturales, Colombia; KU: Museum of Natural History, University of Kansas; MCZ: Museum of Comparative Zoology; MBLUZ: Museo de Biología de la Universidad del Zulia; MHUA: Museo de Herpetología de la Universidad de Antioquia, Colombia; NS: National Fish and Wildlife Laboratories, University of New Mexico; PA: Panama; UIS-MHN: Universidad Industrial de Santander Museo de Historia Natural, Colombia; USNM: National Museum of Natural History (USA);USNMW: National Museum of Natural History (USA) online database; VE: Venezuela.

Locality	State: country	Voucher	Latitude	Longitude	Elevation (m a.s.l.)	Source
Hotel El Lago	Antioquia: CO	MHUA (4709)	05.8996	–074.7233	281	BATRACHIA
Termoelectrica La Sierra	Antioquia: CO	MHUA (0232, 3210)	06.1913	–074.5900	113	BATRACHIA
Finca La Suiza	Antioquia: CO	MHUA (1832–1833, 3179)	06.2996	–074.5317	120	BATRACHIA
Quebrada la Oque, Finca guarda el sol	Antioquia: CO	MHUA (7110)	06.3996	–075.8483	454	BATRACHIA
10 km antes de Sta. Fe de Antioquia	Antioquia: CO	MHUA (3223)	06.4829	–075.7816	532	BATRACHIA
Puerto Berrio	Antioquia: CO	AMNH (39013, 39015, 39021–39025); UMMZ (56506)	06.4892	–074.4108	71	Kluge (1979)
No locality mentioned	Antioquia: CO	MHUA (2642)	06.5079	–075.7483	696	BATRACHIA
Hda. Sta. Barbara	Antioquia: CO	MHUA (675, 1565-1667, 2199, 2410, 2566, 2598, 2599, 3238, 4357, 4819, 4820)	06.5496	–074.6400	600	BATRACHIA
Ciénaga Barbacoas, Finca Casa Loma	Antioquia: CO	MHUA (6444, 6393)	06.7412	–074.2567	57	BATRACHIA
Finca Monteloro	Antioquia: CO	MHUA (3155)	07.2746	–076.4316	202	BATRACHIA
Hacienda Las Mercedes, Bosque Quebradona	Antioquia: CO	MHUA (0093, 0580)	07.4829	–075.2816	171	BATRACHIA
Rio Rayo	Antioquia: CO	MHUA (7519)	07.5079	–075.3733	154	BATRACHIA
No locality mentioned	Antioquia: CO	MHUA (5699)	07.5745	–074.7650	110	BATRACHIA
Finca No hay como Dios, Región Bamba	Antioquia: CO	MHUA (5528)	07.6495	–074.7567	96	BATRACHIA
Estacion Tulenapa, Finca Corpoica	Antioquia: CO	MHUA (2694, 3290, 6238)	07.7829	–076.6732	85	BATRACHIA
Campamento Los Almendros, Augura	Antioquia: CO	MHUA (2288)	07.7912	–076.6483	90	BATRACHIA
Estación Cocorna	Antioquia: CO	MHUA (0675)	06.0413	–074.6400	151	BATRACHIA
Finca La Granja	Antioquia: CO	MHUA (2303)	07.8162	–076.6566	88	BATRACHIA
Parque Recreativo Camacol	Antioquia: CO	MHUA (3639)	07.8829	–076.6316	64	BATRACHIA
Hacienda La Candelaria	Antioquia: CO	MHUA (0038, 1279, 1557)	07.9745	–075.2733	83	BATRACHIA
Vía Caucasia Nechi; Hacienda. La Leyenda	Antioquia: CO	MHUA (1558, 2516, 6031, 6032, 2279, 2336)	08.0079	–075.2483	85	BATRACHIA
Nechi	Antioquia: CO	FMNH (54778–54782)	08.0944	–074.7761	29	Kluge (1979)
Turbo	Antioquia: CO	Uncatalogued	08.0947	–076.7283	0	Lynch & Suárez-Mayorga (2001)
Alto de Quimari	Antioquia: CO	FMNH (61751)	08.1167	–076.3833	411	Kluge (1979)
Primera alternativa para el puerto, entre el rio Necocli y la casa del topógrafo	Antioquia: CO	MHUA (7863)	08.4831	–076.8103	2	BATRACHIA

Continued

Appendix, Table A1. *Continued.*

Locality	State: country	Voucher	Latitude	Longitude	Elevation (m a.s.l.)	Source
Caño Limón, Asoc. Cravo Norte, landfill	Arauca: CO	ICN (27699, 27806, 27807)	06.9378	–071.1525	130	Lynch & Suárez-Mayorga (2001)
Arauca, Hato el Venero's house	Arauca: CO	IAvH (444, 2503, 2504, 2982, 3697–3700, 3902, 3905)	06.9794	–070.7981	123	Lynch & Suárez-Mayorga (2001)
Piscicultura Soplaviento	Atlántico: CO	IAvH (582, 586)	10.3914	–075.1356	11	Lynch & Suárez-Mayorga (2001)
Los Pendales	Atlántico: CO	USNM (152142)	10.6167	–075.2167	59	Kluge (1979)
Polonuevo, Los Charcos	Atlántico: CO	ICN (44414, 44415)	10.7708	–074.8614	90	Lynch & Suárez-Mayorga (2001)
Soledad	Atlántico: CO	ICN (226, 227)	10.9125	–074.7889	46	Lynch & Suárez-Mayorga (2001)
Puerto Colombia	Atlántico: CO	ICN (1021, 1022, 1023, 31549, 31550)	11.0008	–074.9500	18	Lynch & Suárez-Mayorga (2001)
Finca Tierra Prometida; km 15, bajo	Bolívar: CO	UIS-MHN (4812)	05.9496	–074.4567	196	BATRACHIA
Campo Palagua, Estación Vasconia (Ecopetrol S.A.)	Bolívar: CO	UIS-MHN (4788)	06.0663	–074.5567	148	BATRACHIA
Campo Palagua, Finca San Luis	Bolívar: CO	UIS-MHN (4819–4821)	06.0829	–074.5650	133	BATRACHIA
Vereda El Dique	Bolívar: CO	UIS-MHN (4805)	06.1329	–074.5817	143	BATRACHIA
La Raya	Bolívar: CO	USNM (127863, 127864)	08.3394	–074.5389	34	Kluge (1979)
No locality mentioned	Bolívar: CO	MHUA (7365)	08.4162	–074.2317	645	BATRACHIA
Mompos	Bolívar: CO	ICN (26274, 33222)	9.2400	–074.4211	20	Lynch & Suárez-Mayorga (2001)
No locality mentioned	Bolívar: CO	MHUA (0396)	9.2411	–074.7567	8	BATRACHIA
Turbaco, Matute zone; 1 km N San Cristobal	Bolívar: CO	KU (15882, 15883, 15884); ICN (13727, 13728)	9.8917	–075.2539	80	Kluge (1979); Lynch & Suárez-Mayorga (2001)
Santa Rosa	Bolívar: CO	ICN (2101, 2109–2121, 2248–2258, 2267–2269, 2271–2278, 2290–2302)	10.4456	–075.3633	40	Lynch & Suárez-Mayorga (2001)
Santa Catalina, Hacienda El Ceibal	Bolívar: CO	ICN (44416–44461)	10.6233	–075.2417	29	Lynch & Suárez-Mayorga (2001)
Vereda Las Mercedes, Los Balcones farm	Boyacá: CO	ICNMH (38047–38050, 38064)	05.9769	–074.5908	145	Lynch & Suárez-Mayorga (2001)
Puerto Boyacá	Boyacá: CO	UIS-MHN (4843, 4844, 4853)	06.0746	–074.5567	142	BATRACHIA
Vereda La Fiebre, La Barrilera farm	Boyacá: CO	ICNMH (38051–38053, 38066, 38067)	9.7478	–074.8169	6	Lynch & Suárez-Mayorga (2001)
Vereda La Cristalina	Boyacá: CO	ICNMH (38063)	10.3636	–075.4172	130	Lynch & Suárez-Mayorga (2001)
Hacienda El Valle	Caldas: CO	MHUA (5909, 5922)	05.5913	–074.8817	580	BATRACHIA
No locality mentioned	Casanare: CO	?	06.1654	–070.0489	99	Acosta-Galvis & Alfaro (2011)
Vereda Morales	Cauca: CO	CD-UV (1791)	2.9914	–076.4069	1200	Mendez-Narvaez et al. (2014)
El Diamante farm, 15 km S Bosconia	Cesar: CO	NS (110–117, 119–122)	05.8419	–074.3364	301	Kluge (1979)
San Martin Municipality	Cesar: CO	UIS-MHN (0060)	07.9412	–073.6734	41	BATRACHIA
La Gloria, Morales' swamp	Cesar: CO	ICNMH (37308, 37310)	08.5378	–073.7700	13	Lynch & Suárez-Mayorga (2001)
Hacienda Montecarlo	Cesar: CO	ICNMH (37276–37280)	08.5383	–073.6736	82	Lynch & Suárez-Mayorga (2001)
Simaña's swamp	Cesar: CO	ICNMH (18843)	08.5928	–073.7456	42	Lynch & Suárez-Mayorga (2001)
La Jagua, 15 km S Becerril	Cesar: CO	CAS (116294)	9.5678	–073.2781	292	Kluge (1979)
Socorre, upper Río Sinu	Córdoba: CO	FMNH (61168)	07.8500	–076.2833	115	Kluge (1979)
Vereda Tucurá, Quebrada Lavate and Lourdes	Córdoba: CO	ICNMH (39157)	07.9500	–076.2833	103	Lynch & Suárez-Mayorga (2001)
Aeropuerto El Pindo	Córdoba: CO	MHUA (3964)	07.9829	–075.4233	78	BATRACHIA
Damp Urrá	Córdoba: CO	ICNMH (43401–43413)	08.0167	–076.2167	82	Lynch & Suárez-Mayorga (2001)
Tierra Alta, Quebrada El Gallo	Córdoba: CO	ICNMH (39153)	08.1061	–076.0608	187	Lynch & Suárez-Mayorga (2001)
Quebrada La Ron	Córdoba: CO	MHUA (3869)	08.1719	–076.0580	99	BATRACHIA
Tierra Alta	Córdoba: CO	FMNH (61752); UMMZ (135336a-1)	08.1767	–076.0739	75	Kluge (1979)
Catival, upper Río San Jorge	Córdoba: CO	FMNH (61169, 61170)	08.2833	–075.6833	151	Kluge (1979)
Bodegas ICA	Córdoba: CO	MHUA (4496)	08.3162	–075.1483	32	BATRACHIA
Montería, fish farm, Universidad Córdoba	Córdoba: CO	ICNMH (19552–19554)	08.7472	–075.8678	41	Lynch & Suárez-Mayorga (2001)
Lorica	Córdoba: CO	MHUA (3540, 3541, 3550, 3551)	9.1745	–075.9066	19	BATRACHIA
Bosque ITA	Córdoba: CO	ICN 48115	9.2661	–075.8150	43	BATRACHIA
Girardot	Cundinamarca: CO	AMNH (20424)	4.3019	–074.8044	324	Kluge (1979)
Beltran, upper Río Magdalena	Cundinamarca: CO	USNM (152611, 152612)	4.8003	–074.7389	266	Kluge (1979)
Caserio Campo Alegre	La Guajira: CO	MHUA (5604, 5605)	10.9494	–072.7734	146	BATRACHIA
Finca La Necesidad	La Guajira: CO	MHUA (1131)	10.9577	–072.7901	135	BATRACHIA
Rio Rancheria	La Guajira: CO	MHUA (0648, 0649, 0752, 0754)	10.9744	–072.7567	1	BATRACHIA
Maicao, corregimiento Calabacito, El Cerrejón	La Guajira: CO	ICNMH (11824, 11825)	11.0353	–072.6589	140	Lynch & Suárez-Mayorga (2001)
Río Barbacoa, Arroyo de Arenas	La Guajira: CO	UMMZ (54619)	11.2717	–072.9053	47	Kluge (1979)

Continued

Appendix, Table A1. *Continued.*

Locality	State: country	Voucher	Latitude	Longitude	Elevation (m a.s.l.)	Source
Corregimiento Botillero	Magdalena: CO	UIS-MHN (837, 671–682, 684, 686–768, 770, 830–836, 838–848, 874, 875, 877, 889–894, 960, 1277–1294, 1575–1578, 1938–1941)	9.0995	–073.9817	103	BATRACHIA
Curumani	Magdalena: CO	MCZ (21475–21479, 21483)	9.2011	–072.5425	50	Kluge (1979)
Casco Urbano	Magdalena: CO	MHUA (0771)	9.2411	–074.3483	25	BATRACHIA
Guamal Municipality;	Magdalena: CO	MHUA(3903)	9.2495	–074.2317	22	BATRACHIA
Becerril	Magdalena: CO	CAS (116280)	9.7036	–073.2789	138	Kluge (1979)
Plato	Magdalena: CO	AMNH (71042)	9.7911	–074.7975	6	Kluge (1979)
Fundación	Magdalena: CO	UMMZ (46908–46912, 46914–46921)	10.5089	–074.1822	67	Kluge (1979)
Aracataca	Magdalena: CO	ANSP (19779)	10.5914	–074.1861	42	Kluge (1979)
Minca	Magdalena: CO	ICNMH (3863)	11.1428	–074.1075	1530	Lynch & Suárez-Mayorga (2001)
No locality mentioned	Magdalena: CO	UIS-MHN (0459)	11.2327	–073.7150	239	BATRACHIA
El Aranar farm, nr. Bonda	Magdalena: CO	USNM (152715, 152716)	11.2458	–072.1233	45	Kluge (1979)
Puerto Gaitan, Vereda San Miguel, Fundación Yamato	Meta: CO	ICNMHN (38283)	4.2810	–072.0705	151	Lynch & Suárez-Mayorga (2001)
Nearness airport Camilo Daza, Cúcuta	Norte de Santander: CO	Uncatalogued	07.9311	–072.5125	308	Armesto et al. (2009)
Astillero, old town	Norte de Santander: CO	ICNMH (33554–33557)	08.1197	–072.5783	140	Lynch & Suárez-Mayorga (2001)
Landázuri, Hacienda Las Flores	Santander: CO	ICNMH (8796)	06.1367	–073.8811	685	Lynch & Suárez-Mayorga (2001)
Hacienda San Miguel, ciénaga de Cachimbero	Santander: CO	MHUA (2818)	06.3829	–074.3317	127	BATRACHIA
Hacienda Bufalera El Bosque, Campamento El Encanto	Santander: CO	MHUA (3640, 2628, 3185–3201, 3641–3698)	06.4662	–074.3400	109	BATRACHIA
Planta Sebastopol	Santander: CO	UIS-MHN (5124)	06.4746	–074.3900	71	BATRACHIA
Vélez, Carare zone, Campo Capote	Santander: CO	ICNMH (613–615)	06.6192	–073.9147	139	Lynch & Suárez-Mayorga (2001)
Finca La Olinda	Santander: CO	MHUA (1917)	06.6496	–074.0567	83	BATRACHIA
Doradas	Santander: CO	UIS-MHN (0006)	06.8912	–073.5484	172	BATRACHIA
San Vicente	Santander: CO	ANDES-A (1207, 1453, 1541)	06.8953	–073.4303	535	Guarnizo et al. (2015)
El Centro	Santander: CO	AMNH (71043)	06.9358	–073.7514	93	Kluge (1979)
Vereda Marta	Santander: CO	UIS-MHN (4187, 4187)	07.1162	–073.4234	279	BATRACHIA
Cerro La Aurora	Santander: CO	UIS-MHN (3577, 3579)	07.1746	–073.3234	618	BATRACHIA
Sabana de Torres Municipality	Santander: CO	ANDES-A (1533, 1538–1540)	07.3547	–073.4900	145	Guarnizo et al. (2015)
Sabana de Torres Municipality	Santander: CO	UIS-MHN (0515, 0570, 0571)	07.3745	–073.5984	118	BATRACHIA
Vereda Agua Bonita, Reserva Natural El Cabildo Verde, puesto de control 1	Santander: CO	UIS-MHN (3857)	07.3745	–073.4984	141	BATRACHIA
No locality mentioned	Santander: CO	UIS-MHN (3524)	07.4995	–073.7734	42	BATRACHIA
San Marcos, station Crocodilia	Sucre: CO	IAvH (5337, 5703)	08.5453	–075.1833	46	Lynch & Suárez-Mayorga (2001)
San Marcos	Sucre: CO	IAvH (6668, 6669)	08.6578	–075.1316	36	BATRACHIA
Vereda La Caimanera, Sector de la Caimanera	Sucre: CO	IAvH (8235, 8214, 8279, 8215–8218, 8238, 8239, 8243, 8276, 8280)	9.4495	–074.9067	52	BATRACHIA
Colosó, Proyecto Primates	Sucre: CO	IAvH (1167)	9.4950	–075.3528	140	Lynch & Suárez-Mayorga (2001)
Hacienda La Estanzuela, 4 km E Tolu	Sucre: CO	NS (42, 43, 240–243)	9.5225	–075.5833	3	Kluge (1979)
Vereda El Sereno Bajo, 1 km al sur de la Estación Primatológica	Sucre: CO	IAvH (8081, 8086, 8156–8158, 8170)	9.5245	–075.3566	192	BATRACHIA
Vereda El Sereno Alto, Quebrada El Sereno, arriba de la estación	Sucre: CO	IAvH (8062, 8113)	9.5328	–075.3566	192	BATRACHIA
Vereda Macajan, Hacienda Mundo Nuevo	Sucre: CO	IAvH (8360, 8362, 8336, 8363, 8375, 8359, 8374)	9.5745	–075.4483	26	BATRACHIA
San Luis de Onofre [San Onofre]	Sucre: CO	ICNMH (42289)	9.7400	–075.5203	43	Lynch & Suárez-Mayorga (2001)
Espinal, Magdalena Valley	Tolima: CO	MCZ (15063, 15064)	4.1483	–074.8844	333	Kluge (1979)
Honda	Tolima: CO	USNM (152121, 152122, 156888)	05.2050	–074.7364	173	Kluge (1979)
Bitaco, near, on way to Dagua	Valle del Cauca: CO	USNM (151982)	3.5906	–076.6413	1426	USNMW
Municipality of La Victoria	Valle del Cauca: CO	CD-UV (1792)	4.4772	–076.0454	940	Mendez-Narvaez et al. (2014)
Las Tablas	Los Santos: PA	CHP:Herp (0020)	07.7655	-80.2706	37	CHPW
Guanico, Arriba Río Guanico	Los Santos: PA	KU (116361)	07.3406	-80.4961	87	Kluge (1979)
Tonosi	Los Santos: PA	KU (101553–101555)	07.3872	-80.4667	70	Kluge (1979)
Bejuco, Río Bejuco	Panama: PA	AMNH (69766)	08.5733	–079.8842	35	Kluge (1979)
Proyecto Los Islotes, near Los Islotes de Quebro.	Veraguas: PA	CHP:Herp (8501)	07.4014	-80.9231	0	CHPW

Continued

Appendix, Table A1. *Continued.*

Locality	State: country	Voucher	Latitude	Longitude	Elevation (m a.s.l.)	Source
La Florida, 45 km W Coro	Falcón: VE	CIEZAH (401)	11.2333	–070.0667	152	Mijares-Urrutia & Arends (1999)
Bridge on the Chama river, near El Vigía	Mérida: VE	ULABG (5671–5675)	08.6097	–071.6397	183	This study
3.5 km W desvío a Caja Seca	Mérida: VE	ULABG (3292)	9.1208	–071.0567	320	La Marca (1996)
Nearness Arapuey, Sur del Lago de Maracaibo	Mérida: VE	MHNLS (20914–20917)	9.2833	–071.0167	57	This study
Brisas del Chama, 3 km from El Vigía to Caja Seca, just next the bridge	Mérida: VE	ULABG (5711–5713)	08.6133	–071.6247	170	This study
Aprox. 10 km El Vigía, border between Mérida and Zulia	Mérida: VE	ULABG (5319)	08.6979	–071.6931	104	This study
Finca Santa Lucía, road El Vigía-El Quince	Mérida: VE	ULABG (4100)	08.5935	–071.7502	149	This study
Near to Guayabones, 22 km NE de El Vigía	Mérida: VE	CVULA (141)	08.7508	–071.5732	154	This study
Las Virtudes	Mérida: VE	ULABG (1587)	9.1293	–070.9745	605	This study
Sector Vera de Agua, 10 km de El Vigía, road to Sta. Bárbara	Mérida: VE	ULABG (5318, 5320)	08.7119	–071.6992	95	This study
Agropecuaria San Sebastián; Machiques de Perijá	Zulia: VE	MBLUZ (?)	9.8676	–072.3996	100	Infante-Rivero & Velozo (2015)